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THIRTY-SIX YEARS OF CHANGE IN AN EASTERN HEMLOCK-WHITE PINE STAND IN WESTERN MASSACHUSETTS

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ABSTRACT. The vegetation of an eastern hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*) stand at Arcadia Wildlife Sanctuary, Easthampton, Massachusetts, was studied in 1963, in 1975, and again in 1998–99. Hemlock remained dominant from 1963 through 1999 despite extensive mortality of smaller stems. White pine and two minor canopy species, red maple (*Acer rubrum*) and black cherry (*Prunus serotina*), also declined. Changes in stem size structure of tree populations within the stand may have reflected in part increasing stand maturity, resulting in fewer and larger trees. In addition, low recruitment into the canopy and numerous tree deaths between 1963 and 1975 occurred at a time of widespread regional drought. Tree seedlings, nearly absent from the site in 1963, were well established by 1975, approximately five years after rainfall amounts returned to normal levels, but extensive mortality of canopy trees continued through 1998, particularly hemlock and black cherry. Tree deaths during this latter period coincided with defoliation by gypsy moths (*Lymantria dispar*) and wind throw during severe ice storms in the winter of 1996–1997. Hemlock wooly adelgids (*Adelges tsugae*) were not observed at the site until after the 1998 sampling; thus this study may serve as a baseline for assessing adelgid damage in the future.

Key Words: hemlock-white pine forest, *Tsuga canadensis*, *Pinus strobus*, hemlock wooly adelgid (*Adelges tsugae*)

The roles of American hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) and their interrelationships within New England forests have been studied for more than a century. Nichols (1913, 1935) considered hemlock a characteristic tree of the "climatic climax forest" of the region and white pine a regular though minor component of this forest, with individual pine trees sometimes present as relicts of earlier stages of succession. Bromley (1935) presented historical evidence that precolonial forests of southern New England included three distinct vegetation types, forming oak, white pine, and northern forest (hemlock-northern hardwoods) regions. In the white pine region, white pine appeared as a superdominant tree or group of trees emerging from a canopy of hardwoods (Bromley 1935; Hibbs 1982). Nonetheless Bromley agreed with Nichols that white pine-hemlock formed the climatic climax of the area.

More recent studies based on presettlement tree surveys and spatial analysis (Cogbill 2000; Cogbill et al. 2002) suggest, however, that the importance of hemlock and pine in New England was overestimated, and that within the precolonial landscape, a northern hardwood forest dominated by beech (*Fagus grandifolia*) originally was separated from a more southerly "central hardwood" forest dominated by oaks (*Quercus* spp.). Hemlock was most prevalent in the uplands, especially in Massachusetts to the west of the Connecticut River, while white pine was "remarkably uncommon" in the uplands and scarce to absent in western Massachusetts. In addition, studies based largely at Harvard Forest in Petersham, Massachusetts (Foster et al. 1992; McLachlan et al. 2000) led to the conclusion that sites characterized by hemlock with emergent white pines may give "the impression of great size and stability" but may in fact represent complex patterns of response to anthropogenic disturbance that do not reflect presettlement conditions. Previous forest composition was distinctive for each of the Harvard Forest sites and included a range of successional stages including various hardwood species as well as hemlock and white pine. Over time, forest composition at the sites converged on hemlock as a result of selective logging, wind throw, and outbreaks of pathogens such as the fungus causing chestnut blight.

A hemlock-white pine stand now included as a part of Arcadia Wildlife Sanctuary, a property owned by the Massachusetts Audubon Society in Easthampton, Massachusetts, has been studied extensively three times over a 36-year interval. The stand was first investigated during summer, 1963, by M. R. Castelli as part of a broader examination of the successional role of hemlock in the Connecticut River Valley in Massachusetts (Castelli 1964). The Arcadia site was chosen because the forest, on preliminary inspection, seemed an example of a hemlock-white pine stand that was undergoing transition to a "hemlock consociation," a geographic variant of the regional climax vegetation with only hemlock as a dominant (Oosting 1956). The stand was believed to represent a mid-successional stage and was compared with both younger and older sites. The 1963 sampling was conducted after the onset of widespread regional drought (see Figure 1 in Holland et al. 2000, which was based on precipitation data available from the National Oceanic and Atmospheric Administration website: http://www.ncdc.noaa.gov), and tree seedlings of any species were virtually absent from the stand.

The stand was studied again during fall, 1975, by W. B. Coleman (Coleman, unpubl. ms.). By 1975, total precipitation in the area had returned to predrought levels (Figure 1 in Holland et al. 2000) and tree seedlings within the stand were abundant.

A third intensive sampling of the site was carried out during 1998–1999 by B. Garcia Bailo (Garcia Bailo, unpubl. ms.). This sampling was intended in part to document stand composition prior to an anticipated infestation by the hemlock wooly adelgid (*Adelges tsugae*), an invasive exotic insect that had already caused widespread damage to hemlocks in forests immediately to the south (Orwig and Foster 1998).

The present study is a synthesis and comparison of vegetation data from 1963, 1976, and 1998–1999. Specific goals were: (1) to identify and census each tree in the stand at each sampling period; (2) to establish the population size structure of each tree species at each sampling period; (3) to document seedling establishment and herbaceous cover at each sampling period; and (4) to attempt to determine long-term patterns of vegetational change within the stand.

MATERIALS AND METHODS

Study site. The Arcadia site is located in Easthampton, Massachusetts, on an upper Connecticut River terrace north of Mount Tom State Reservation and approximately 2000 m southwest of Hulbert's Pond, an ancient oxbow of the Connecticut River (U.S. Geological Survey, Easthampton, MA topographic map, 1964 edition). The site was acquired by the Massachusetts Audubon Society as part of Arcadia Wildlife Sanctuary in the mid-1960s. Land use prior to the establishment of hemlock-white pine forest is uncertain, although Coleman (unpubl. ms.) surmised, based on evidence from conversations with a previous owner of the site and the presence of stumps of hardwoods, including American chestnut (*Castanea dentata*) at its periphery, that it may have been an open woodland that was sporadically cut for fuel. Coleman believed disturbance had been minimal since around 1900. Through the period 1963–1999, the hemlock-white pine stand occupied approximately 0. 36 ha and was roughly oval, 100 m long and 50 m across at its widest point. Its general limits were defined by two brooks, Hemlock Brook to the north and an unnamed brook to the south. These streams merged at the eastern margin of the site. The slippery clay banks of Hemlock Brook and a wetland surrounding the southern brook made access difficult, and thus the forest had been only slightly disturbed by human activities. The forests adjacent to the site originated on land that was cleared for agriculture through the early 1900s and were mostly cutover hardwoods in earlier stages of succession. These tracts reportedly burned prior to the beginning of the study (Arcadia Wildlife Sanctuary staff, pers. comm.) but the fires did not enter the hemlock-white pine stand.

Aside from drought, two disturbances with regional impacts may have affected the stand between 1963 and 1998–1999. Defoliation resulting from heavy infestations of the gypsy moth (*Lymantria dispar*) occurred in adjacent forests in the late 1970s and early 1980s. Vegetation studies associated with breeding bird surveys in 1994 and 1995 indicated a shift in canopy dominance after 1975 from oak species to white pine (Mooney, unpubl. ms., Arcadia Wildlife Sanctuary; Neelon, unpubl. ms., Arcadia Wildlife Sanctuary); the degree to which the moths affected the hemlock-white pine stand was not determined at the time. In addition, wind throw during two major ice storms during winter, 1996–1997, toppled a grove of hemlocks east of the Arcadia stand and caused minor tree loss in the stand itself.

White-tailed deer (*Odocoileus virginianus*) are seen regularly at Arcadia Wildlife Sanctuary, but browse effects on the vegetation were not observed in vegetation studies associated with the breeding bird survey, in studies of the herb stratum of nearby floodplain forests (Holland and Burk 1984; Holland et al. 2000), or by trained sanctuary staff (D. McLain, pers. comm.). Hemlock wooly adelgids were first observed in the stand after the 1998 sampling.

Sampling in 1963. During spring, 1963, the entire stand was divided along lines laid out with a compass to form a grid of 144 quadrats, each 5 m × 5 m. Each tree was identified to species and its diameter at 1.5 m above ground (DBH) recorded in one of six diameter size classes: 2.5–10.1 cm, 10.2–20.2 cm, 20.3–30.4 cm, 30.5–40.5 cm, 40.6 cm–58.3 cm, and 58.4 cm and larger. A map was then prepared indicating the position, identity to species, and size class of each tree. Ages of representative trees of each species in each size class were determined by counting annual rings in a core taken at 4.5 feet above ground with an increment borer. Frequency [(number of occupied quadrats ÷ total number of quadrats sampled) × 100] was determined for each herbaceous species and woody seedling in the stand.

Sampling in 1975. During fall, 1975, an attempt was made to re-locate each tree on the 1963 map, and DBH was recorded as before. A grid of 5 m × 5 m quadrats was laid out across the stand and the number of seedlings of each tree species in each of 144 quadrats was recorded. All woody stems less than 60 cm height were considered seedlings. Woody stems over 60 cm height but less than 2.5 cm diameter were considered saplings. Because this study was initiated late in the growing season, herbaceous species were listed but not sampled.

Sampling in 1998–1999. Between May and late September, 1998, another attempt to re-locate trees on the 1963 map and to measure the DBH of each tree in the stand was carried out. Snags and standing dead trees were omitted from the survey, and trees indicated on the map but not found in the stand were assumed to have fallen and decomposed or to have been removed from the site as firewood. Because tree seedlings were much more numerous than in previous sampling periods, tree seedlings were not counted throughout the entire stand. Instead, during summer, 1999, a grid of 1 m × 1 m quadrats was laid out across the stand, and tree seedlings, defined as in 1975, were counted in each of 100 quadrats placed at regular intervals along baselines through the stand in an attempt to sample all sections of the stand proportionately.

Relative dominance [(basal area of an individual species ÷ basal area of all species) × 100] and relative density [(number of individuals of a species ÷ number of individuals of all species) × 100] were calculated (Barbour et al. 1998; Mueller-Dombois and Ellenberg 1974). Basal area was determined according to Phillips (1959). Relative densities and relative frequencies [(frequency of a species × 100) ÷ sum of frequencies of all species] of tree seedlings were calculated for both the 1975 and the 1998–1999 seedling data. Frequency was also determined for each herb species occurring in the quadrats. Because determinations of frequency are influenced by quadrat size (Mueller-Dombois and Ellenberg 1974), frequency data for the smaller quadrats used in 1999 cannot be compared with prior years. Nomenclature follows Sorrie and Somers (1999).

RESULTS

Sampling in 1963. At the beginning of the study, hemlock was the dominant and most numerous canopy tree species in the stand (Table 1; Figures 1 and 2). Most hemlocks occurred in the three lower size classes (Figure 3), with nearly 40% of the trees ranging from 10.2–20.1 cm DBH. Only six hemlocks were greater than 30.4 cm in diameter. The

Table 1. Total number (n), density (stems/ha) and basal area (m^2/ha) of trees of each species and total number, density, and basal area of trees of all species present at each study period.

	Year								
	1963			1975			1998		
Species	n	Density	Basal Area	n	Density	Basal Area	n	Density	Basal Area
Hemlock	209	581	22.6	169	469	27.8	114	317	40.1
White pine	45	125	15.3	37	103	21.4	27	75	27.1
Red maple	43	119	2.3	37	103	3.5	34	94	5.8
Black cherry	15	42	0.6	11	31	0.6	3	8	0.3
TOTAL	312	867	40.8	254	706	53.3	178	494	73.3

largest hemlocks ranged from 61 to 63 years of age in 1963 and tended to cluster near the center of the site, with younger and smaller hemlocks concentrated towards the margins.

White pine, which was slightly more numerous than red maple (Table 1; Figure 1), ranked second in relative dominance to hemlock (Figure 2). White pines were better represented in the larger size classes than other tree species, with more than 40% of the trees over 30.4 cm in diameter (Figure 3). The oldest pines ranged from 57 to 68 years in age and were scattered throughout the site.

Red maple (*Acer rubrum*) occurred only in the lower size classes and black cherry (*Prunus serotina*) was a minor stand component. The largest maples ranged from 25–27 years of age, the largest black cherries from 20–29 years.

Tree seedlings and saplings were very scarce, occurring only near the stand's periphery. The herbaceous stratum was poorly developed, with most herbs occurring in patches under breaks in the canopy. The most frequent herbs were *Dryopteris carthusiana*, *Maianthemum canadense*, *M. racemosum*, *Trillium erectum*, and *Trientalis borealis*.

Sampling in 1975. Trees of all four species declined in number between 1963 and 1975 (Table 1). Because of the near absence of seedling and sapling trees in 1963, we doubt that any new stems entered the canopy size classes, but we cannot be certain this was the case. Changes in the number of individual trees within each size class may have occurred either from mortality or the transition of individual trees into or out of that size class resulting from growth. Hemlocks decreased by 19% with the highest declines in the two smaller size classes (Figure 3). White pine decreased by 18% with declines in numbers also greater

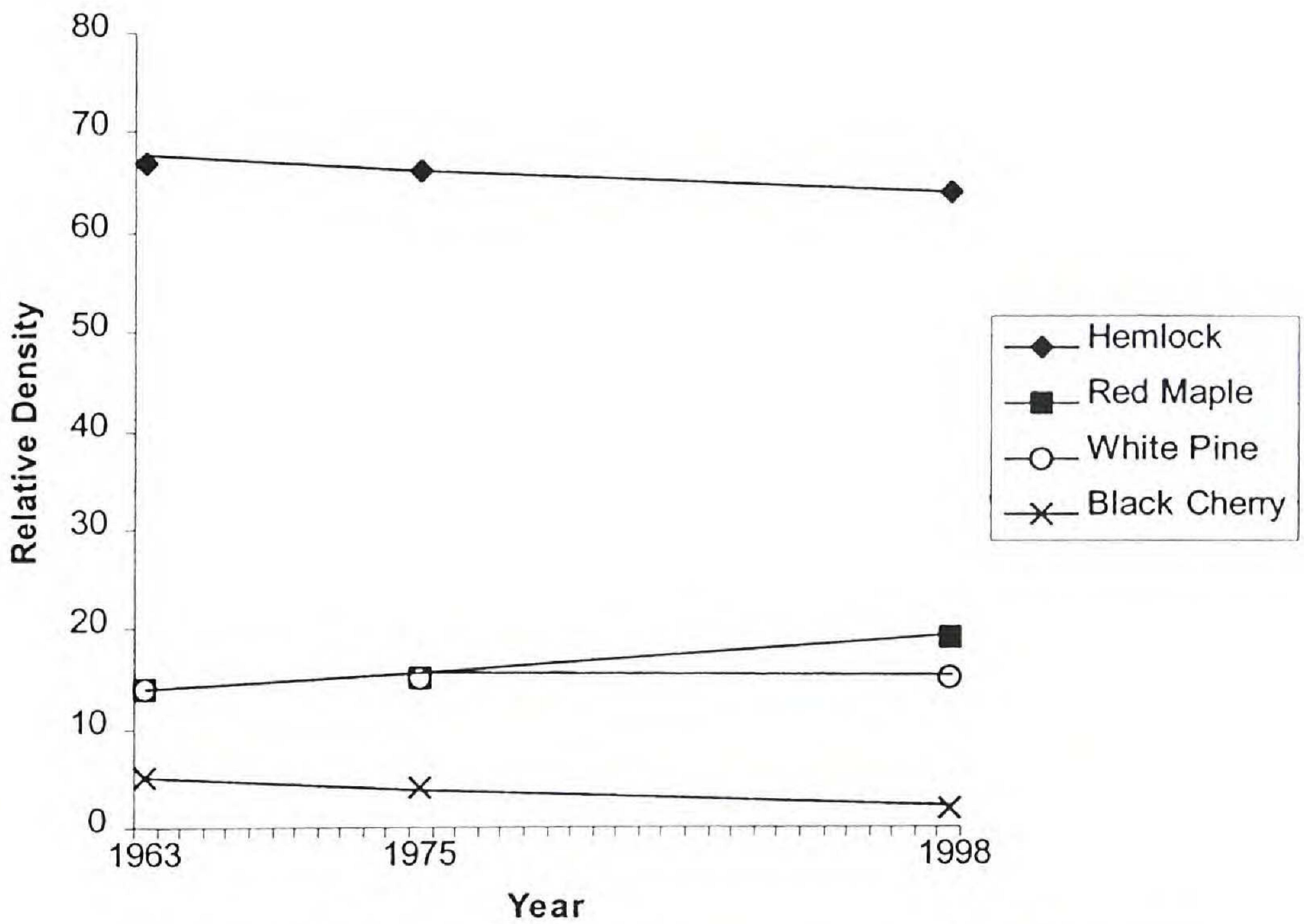

Figure 1. Relative density of each tree species at each study period.

in the two lower size classes; however the number of trees over 30.4 cm diameter rose to more than 70% of the white pine population. Red maple declined by 14% and black cherry by 27%; in both species the lower size classes sustained the greatest loss of numbers. Despite losses through mortality, basal areas of all species except black cherry increased through the period (Table 1). Tree seedlings and saplings also increased, especially near the borders of the stand, with red maple, hemlock, and black cherry particularly numerous (Table 2). White pine seedlings were still infrequent. *Lycopodium clavatum*, *Dryopteris carthusiana*, and *Mitchella repens* were the most frequent herbs, along with *Polystichum acrostichoides*, *Maianthemum canadense*, *M. racemosum*, *Trientalis borealis*, and *Aster divaricatus*.

Sampling in 1998–1999. By the end of the 36-year study period, total tree density had declined by 45% (Table 1). As in 1975, we were uncertain whether any stems had entered the canopy size classes or not. Mortality was greater in hemlock than pine, with slightly over half (55.6%) of the original number of hemlocks and three fourths (75.8%) of the original number of pines represented in the stand. Nonetheless, the relative density and relative dominance of hemlock and white pine remained essentially constant (Figures 1 and 2). Approximately two-thirds (62.8%) of the original number of red maple trees were present,

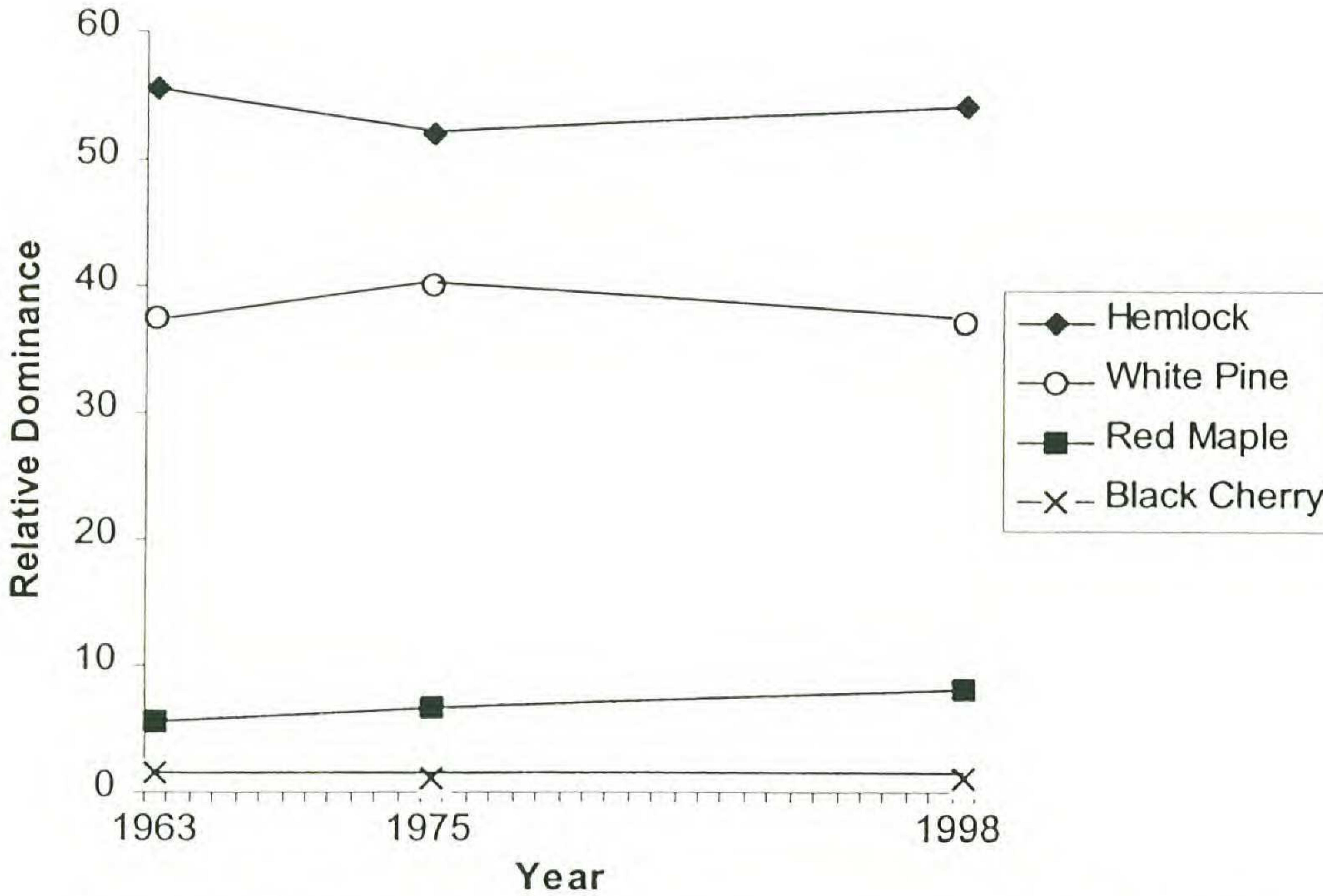

Figure 2. Relative dominance of each tree species at each study period.

but only a few black cherries persisted, most having died in the interval 1975–1998 (Table 1). During the 36-year interval, the population structure of all tree species shifted from a predominance of trees in smaller DBH classes to a predominance of trees in higher DBH classes; hence all species were represented by fewer but larger specimens (Table 1; Figure 3). Basal areas of both hemlock and white pine increased more than 75% (Table 1).

Total seedling density was over five times greater than in 1975. Red maple seedlings remained most numerous. White pine seedlings had increased, comprising over 30% of the seedling population, and surpassing hemlock seedlings in abundance. Black cherry seedlings did not occur in the 1999 sampling. While individual plants of *Dryopteris carthusiana* occurred throughout the site, the most abundant herbaceous species in 1999 was *Dennstaedtia punctilobula*, which formed colonies in several patches under light gaps. *Trientalis borealis*, *Medeola virginiana*, *Maianthemum canadense*, *Lycopodium obscurum*, *Trillium erectum*, and *Gaultheria procumbens* were also present at frequencies above 5%.

DISCUSSION

Long-term studies of vegetation at specific sites are generally scarce (Runkle 1990), although research in hemlock-white pine stands may be

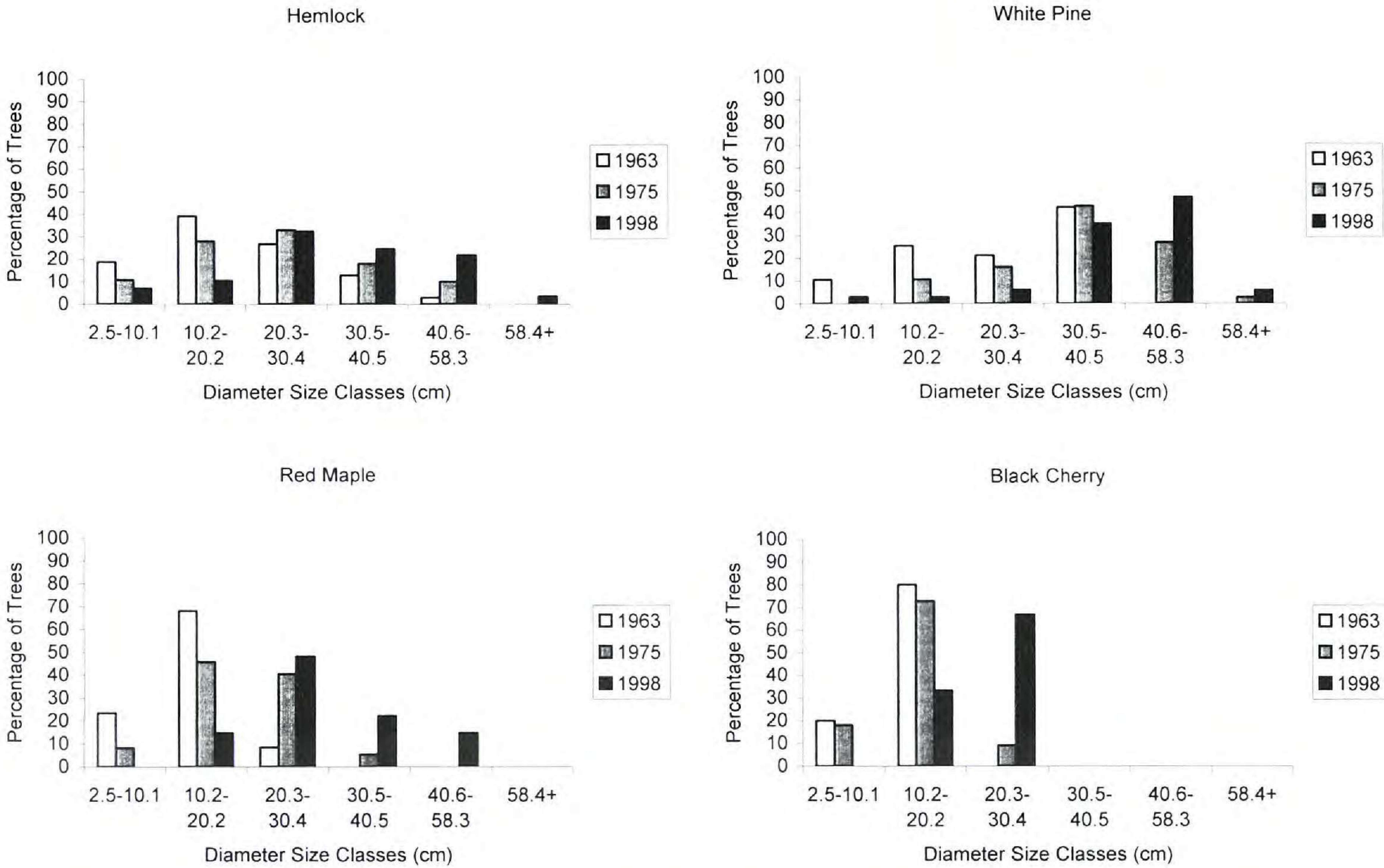

Figure 3. Percent of trees of each species represented in each of six diameter size classes at each study period.

Table 2. Density (D, stems/ha) and relative density (RD) expressed as percent of tree seedlings in 1975 and in 1998. *mostly *Quercus* spp.

	Year			
	1975		1998	
Species	D	RD	D	RD
Hemlock	822	27.5	2700	17.1
White pine	22	0.7	4800	30.1
Red maple	1392	46.6	7200	45.6
Black cherry	553	18.5	—	—
Other species*	200	6.7	1100	7.0

better represented than in most forest types. Lutz (1930), for example, described a hemlock consociation, defined by the predominance of hemlock in the larger size classes, from the Heart's Content forest in northwestern Pennsylvania. Hemlock seedlings were also abundant in these stands, which Lutz believed represented a stable "environmental or physiographic climax." Further investigations of Pennsylvania forests considered mortality of large or overstory hemlocks among the chief effects of the regional droughts of the 1930s (Hough and Forbes 1943). A reinvestigation of the Heart's Content forest in 1978, fifty years after the initial sampling (Whitney 1984) found that extensive browsing by white-tailed deer had greatly reduced hemlock seedlings and saplings but had little effect on hemlock trees, even in the smaller size classes. During the fifty-year interval, the estimated hemlock density had more than doubled to nearly 500 stems/ha. Similarly, McLachlan et al. (2000) examined four stands dominated by hemlock at the Harvard Forest, Petersham, Massachusetts in 1995, and compared them with similar adjacent plots that were sampled in 1937. By the early 20th century, the stands had moved from earlier successional hardwoods to hemlock as a result of disturbances including chestnut blight and logging. Between 1937 and 1995, the stands became "more massive" and increasingly dominated by hemlock. Within each stand, hemlock densities nearly or more than doubled during the 58-year interval, increasing to a stand average of over 1000 stems/ha, with extensive hemlock regeneration in the understory.

The history of the Arcadia site through the early 20th century may have been similar to that at Petersham. However, in contrast to trends observed at Petersham and Heart's Content, stem densities of all tree species at Arcadia declined from 1963 through 1998, with numerous tree deaths and low recruitment of canopy trees. Over the period 1978–1986, Runkle (1990) also found very high mortality for small tree stems and lower mortalities for intermediate and larger trees in an older hemlock stand in upstate New York. He suggested that an acceleration of a previously noted decline of small stems over the eight-year interval may have resulted from browsing by white-tailed deer and the severe effects of droughts in 1982 and 1983 on younger trees.

Prolonged droughts can result in the deaths of "mesic" forest species (White 1979), especially for shallow-rooted trees such as hemlock (Hough and Forbes 1943; Runkle 1985, 1990). Tree deaths in the Arcadia stand between 1963 and 1975 coincided with the regional drought that ended in the late 1960s (Figure 1 in Holland et al. 2000). Castelli (1964) observed "few dead old trees" in 1963, but also noted the lack of seedlings and saplings in the stand and estimated that no trees had entered the canopy for at least twelve years. Coleman (unpubl. ms.) was able to census a total of 65 standing or recently fallen dead trees during fall, 1975. Of these, only six stems had diameters greater than 30.5 cm. She observed that most tree deaths occurred in the densest portions of the stand. Tree deaths between 1975 and 1998 could have resulted in part from gypsy moth damage. Although gypsy moths normally feed on deciduous tree species, primarily oaks, during large population outbreaks they may also eat needles of hemlock and other conifers (Leonard 1981). In addition, the narrow width of the stand and its position, surrounded by shorter deciduous vegetation, may have made it particularly vulnerable to wind-throw during ice storms. Whatever the cause, substantial hemlock mortality in the stand was occurring years before the arrival of hemlock wooly adelgids.

This study may serve as a baseline for assessing the effects of the hemlock wooly adelgid on regional forests. Given the discovery of adelgids at the Arcadia site after the 1998 sampling and predictions that adelgid damage will result in"unprecedented hemlock loss" throughout the entire range of hemlock (Orwig et al. 2002), the floristic composition and the size structure of the canopy trees within the stand are likely to change in the near future. In adelgid-infested stands in southern Connecticut, smaller hemlock trees suffered greater mortality than larger trees (Orwig and Foster 1998). In the Connecticut stands with moderate to high hemlock mortality, black birch (*Betula lenta*) was the most important woody invader along with red maple, black cherry, and various oaks. Similarly, Kizlinski et al. (2002) found that sites infested with hemlock wooly adelgid showed higher light levels than undamaged sites, along with increased frequencies and cover of several components of the understory vegetation, particularly red maple and black birch.

The greatly increased numbers of seedlings of white pine, red maple, and oak in 1998–1999 at the Arcadia site, especially the higher densities of seedling white pines (Table 2), and the recent expansion in the herbaceous stratum of *Dennstaedtia punctilobula*, a fern known to spread aggressively in open wooded sites and clearings (Nauman and Evans 1993), all suggest that light levels on the forest floor have already increased. In forests adjacent to the Arcadia stand, white pine, red maple, red oak, and black birch are prominent in the canopy (Neelon, unpubl. ms.), with all but black birch well represented in the understory (Mooney, unpubl. ms.). Within the Arcadia stand, as the hemlocks are increasingly damaged by adelgids, white pine, red maple, red oak, and black birch can be expected to increase, their numbers augmented from nearby seed sources. In time, these species should replace hemlocks in the canopy. The SORTIE model of Pacala et al. (1993, 1996) has been used to predict patterns of forest succession in transition oak-northern hardwood forests in northeastern North America. The model examines the dynamics of nine potentially dominant or subdominant tree species, including hemlock, white pine, red maple, red oak, and black cherry. It shows red oak and black cherry dominant early in the sequence and hemlock and beech dominant in its final stages (Pacala et al. 1996). This and similar models may be helpful in predicting long-term change in forests similar to the Arcadia stand, where fewer tree species are present and one potential dominant may have been eradicated. In the shorter term, however, as the older white pines continue to grow in height, the stand at Arcadia may for a time resemble the precolonial forests of the region, where the pines were found as emergent or superdominant trees surrounded by a lower canopy of hardwoods (Bromley 1935; Hibbs 1982).

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LITERATURE CITED

BARBOUR, M. G., J. H. BURK, W. D. PITTS, F. S. GILLIAM, AND M. W. SCHWARTZ. 1998. Terrestrial Plant Ecology, 3rd ed. Addison Wesley Longman, Inc., Menlo Park, CA.

BROMLEY, S. W. 1935. The original forest types of southern New England. Ecol. Monogr. 5: 61–89.

CASTELLI, M. R. 1964. The role of hemlock, *Tsuga canadensis*, in various stages of secondary succession in the Northampton-Amherst area. M.A. thesis, Smith College, Northampton, MA.

COGBILL, C. V. 2000. Vegetation of the presettlement forests of northern New England and New York. Rhodora 102: 250–276.

———, J. BURK, AND G. MOTZKIN. 2002. The forests of presettlement New England, USA: Spatial and compositional patterns based on town proprietor surveys. J. Biogeogr. 29: 1279–1304.

FOSTER, D. R., T. M. ZEBRYK, P. SCHOONMAKER, AND A. LEZBERG. 1992. Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England. J. Ecol. 80: 773–776.

HIBBS, D. E. 1982. White pine in the transition hardwood forest. Canad. J. Bot. 60: 2046–2053.

HOLLAND, M. L. AND C. J. BURK. 1984. The herb strata of three Connecticut River oxbow swamp forests. Rhodora 86: 397–415.

———, ———, AND D. MCLAIN. 2000. Long-term vegetation dynamics of the lower strata of a western Massachusetts Oxbow Swamp Forest. Rhodora 102: 154–174.

HOUGH, A. F. AND R. D. FORBES. 1943. The ecology and silvics of forests in the high plateaus of Pennsylvania. Ecol. Monogr. 13: 299–320.

KIZLINSKI, M. L. D., A. ORWIG, R. C. COBB, AND D. R. FOSTER. 2002. Direct and indirect ecosystem consequences of an invasive plant on forests dominated by eastern hemlock. J. Biogeogr. 29: 1498–1503.

LEONARD, D. E. 1981. Bioecology of the gypsy moth, pp. 9–29. *In*: C. C. Doane and M. L. McManus, eds., The Gypsy Moth: Research Toward Integrated Pest Management. Tech. Bull. 1584, U.S. Dept. Agriculture, Washington, DC.

LUTZ, H. J. 1930. Vegetation of Heart's Content. Ecology 11: 1–29.

MCLACHLAN J. S., D. R. FOSTER, AND F. MENALLED. 2000. Anthropogenic ties to late successional structure and composition in four New England hemlock stands. Ecology 81: 717–733.

MUELLER-DOMBOIS, D. AND H. ELLENBERG. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York.

NAUMAN, C. E. AND A. M. EVANS. 1993. *Dennstaedtia*, pp. 199–201. *In*: Flora of North America Editorial Committee, eds., Flora of North America North of Mexico, Vol. 2. Pteridophytes and Gymnosperms. Oxford Univ. Press, Oxford and New York.

NICHOLS, G. E. 1913. The vegetation of Connecticut II. Virgin forests. Torreya 13: 199–215.

———. 1935. The hemlock-white pine-northern hardwood region of eastern North America. Ecology 16: 403–422.

OOSTING, H. J. 1956. The Study of Plant Communities: An Introduction to Plant Ecology. W. H. Freeman Co., San Francisco, CA.

Orwig, D. A. and D. R. Foster. 1998. Forest response to the introduced hemlock wooly adelgid in southern New England, USA. J. Torrey Bot. Soc. 125: 60–73.

———, ———, and D. I. Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock wooly adelgid. J. Biogeogr. 29: 1475–1487.

Pacala, S. W., C. D. Canham, and J. A. Silander Jr. 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Canad. J. Forest. Res. 23: 1980–1988.

———, ———, ———, J. Saponara, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: Estimation, error analysis, and dynamics. Ecol. Monogr. 66: 1–43.

Phillips, E. A. 1959. Methods of Vegetation Study. Holt and Dryden, New York.

Runkle, J. R. 1985. Disturbance regimes in temperate forests, pp. 17–33. *In*: S. T. A. Pickett and P. S. White, eds., The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, FL.

———. 1990. Eight years change in an old *Tsuga canadensis* woods affected by beech bark disease. Bull. Torrey Bot. Club 117: 409–419.

Sorrie, B. A. and P. Somers. 1999. The Vascular Plants of Massachusetts: A County Checklist. Div. Fish. Wildl., Massachusetts Natural Heritage and Endangered Species Program, Westborough, MA.

White, P. A. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. 45: 229–299.

Whitney, G. G. 1984. Fifty years of change in the arboreal vegetation of Heart's Content, an old-growth hemlock-white pine-northern hardwoods stand. Ecology 65: 403–408.